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Pollution Impacts at the Stand and Ecosystem Levels

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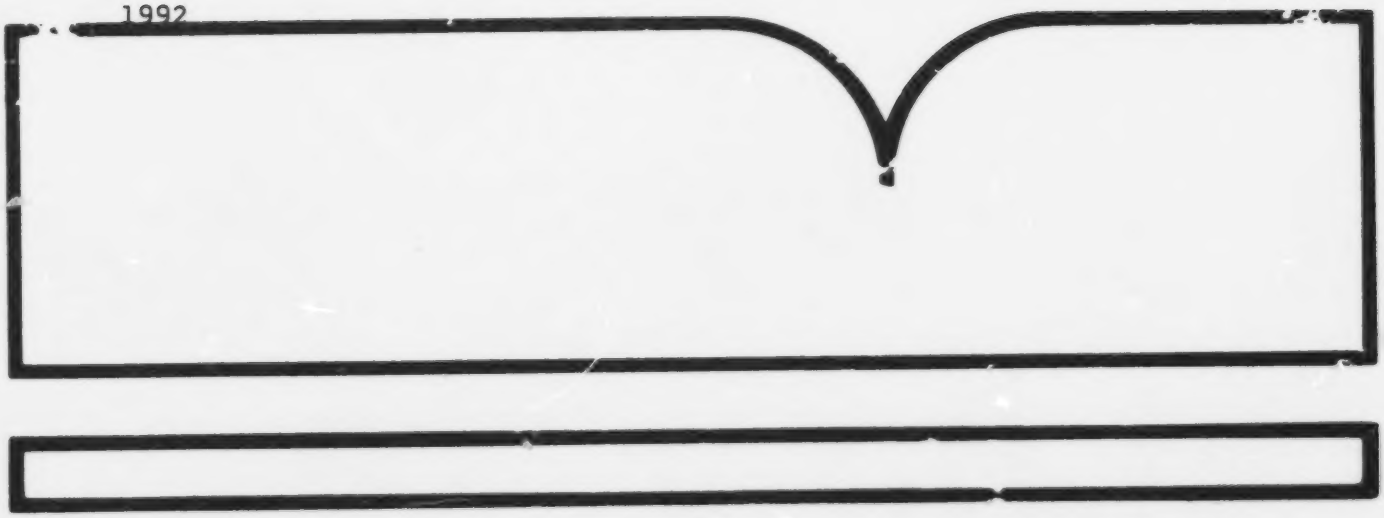

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The responses of forests to pollutants depend on the sensitivity of individual trees and species to the pollutants, and on complex interactions between trees, the environment, and other organisms. Impaired growth in one individual or species may represent an opportunity for increased growth for other trees or species. An ecosystem perspective is necessary for a full assessment of pollutant impacts, but the response of forest to air pollutants remains poorly understood. In this chapter, we discuss important aspects of forests at the level of stands and ecosystems , as a foundation for the regional case studies presented in later chapters. Many key aspects of the effects of pollution at the stand and ecosystem level remain unexplored across the West; this chapter develops a framework for understanding pollution impacts, summarizes what is currently known, and provides some speculation where information is not available.

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CHAPTER 6

POLLUTION IMPACTS AT THE STAND AND ECOSYSTEM LEVELS

Dan Binkley, Terry D. Droessler, and Jeffrey Miller

The responses of forests to pollutants depend on the sensitivity of individual trees and species to the pollutants, and on complex interactions between trees, the environment, and other organisms. Impaired growth in one individual or species may represent an opportunity for increased growth for other trees or species. An ecosystem perspective is necessary for a full assessment of pollutant impacts, but the response of forests to air pollutants remains poorly understood. Smith (1990) stated that knowledge is strongest about the relation between pollution and individual trees, weaker at the level of stands of trees, and weakest at the ecosystem level. The effects of pollutants at an ecosystem level must be evaluated in terms of deviations from expected patterns of change within forests over time. Defining "expected trends" is a major challenge, as pervasive change is basic to the nature of forests (Oliver and Larson 1990), and classic theories regarding ecosystem succession toward predictable future states are seriously in doubt (Botkin 1989). In this chapter, we discuss important aspects of forests at the level of stands and ecosystems, as a foundation for the regional case studies presented in later chapters. Many key aspects of the effects of pollution at the stand and ecosystem level remain unexplored across the West; this chapter develops a framework for understanding pollution impacts, summarizes what is currently known, and provides some speculation where information is not available.

Current perspectives diverge on the nature of forests, ranging from characterizations of forests as anarchies of competing organisms to tightly integrated systems. Oliver and Larson (1990) advocate a "mechanistic" view of forests in contrast to "systems" view; they prefer the term "stand" to "ecosystem" (which does not appear in their index). In contrast, Smith (1990) states that the goal of his book was to describe the interactions of pollutants with forests expressly at the ecosystem level. This chapter takes a middle ground, focusing on stands when discussing patterns of forest change over time, and on ecosystems when including complex interactions between species, pollution, and environmental factors. Given the current state of knowledge, the discussion focuses on describing the important pieces of the puzzle, with only a few examples available to illustrate many points. Basic patterns of tree growth and stand development in the absence of pollution

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impacts are described, and then contrasted with pollution-affected forests. We conclude with a synthesis of current thinking about stand development and ecosystem responses to varying degrees of pollution stress.

Growth

The production of biomass in forests depends on the interception of light by leaves, and on the conversion of intercepted light energy into carbohydrates. The efficiency of this conversion depends largely on the availability of water since leaves under drought stress intercept light, but fail to produce carbohydrates. Some of the carbohydrates produced from photosynthesis are respired as CO_2 as part of the cost of synthesizing and maintaining plant tissues; the remaining carbohydrates form new leaves, stems, branches, and roots. The productivity of forests differ because of differences in stand leaf area and resultant light interception, and the efficiency of producing carboyhydrates from intercepted light. These differences depend in large part on climate, soils, species composition, and history of disturbances.

Measurements of tree growth include changes in tree diameter (or radius), height, volume, and biomass. Volume and biomass growth continue at high rates through most of the lifespan of trees that maintain dominant positions in the canopy. The growth of suppressed trees usually declines as the canopies of dominant trees expand, often leading to death of suppressed trees. The increase in height, radius, and volume of a Douglas-fir (Pseudotsuga menziesii) tree on a dry site in Oregon illustrates a common pattern (Figure 6.1a; data provided by Joe Means, U.S.D.A. Forest Service). Trees increase in height relatively rapidly; the Douglas-fir at age 150 years had attained half of the total height reached by age 400 years. The midpoint in radius did not occur until about age 200 years, which is later than expected and may indicate that the tree experienced strong competition from other trees during the first century. The accumulation of stem volume was very slow for almost 300 years, with about half the volume accumulating during the last century. In terms of annual growth, the maximum height growth occurred at about age 50 (Figure 6.1b), while the maximum growth rate for radius (age 200) and volume (age 300) occurred much later. Foresters typically evaluate growth in terms of when the maximum mean annual increment (volume divided by age) occurs. Even after 400 years of growth, the mean annual increment of this Douglas-fir was increasing.

Patterns in stand growth differ substantially from those of individual dominant trees. Dominant trees often continue increasing in annual growth long after the stand has reached its maximum growth and begun to decline in growth rate. The current volume increment for the Douglas-fir tree in Figure 6.1 can be contrasted with the expected current volume increment for the whole stand

(Figure 6.2; derived from normal stand tables of McArdle et al. (1961) for a site index of 40 m at 100 years). The peak volume growth for such stands occurs near age 50, contrasted with the single tree's peak near age 300. This example illustrates the complexities faced in determining trends in growth for single trees, for stands of trees, and any role that pollution may play in driving these trends.

The rates and patterns of stand growth also depend on the species present, further complicating the task of differentiating pollutant impacts from normal trends. For example, a stand of nitrogen-fixing red alder (Alnus rubra) on a very fertile site on the coast of Oregon showed very rapid biomass accumulation and growth soon after stand initiation; stand growth rates began to decline at about age 30 (Figure 6.3, from Binkley and Greene 1983). Despite the reduction in stand growth rate after age 30, the growth rate of dominant trees continued to increase with no peak in sight by age 55 (data not shown). A conifer stand on the same site grew more slowly initially, but maintained high growth rates for a longer period, resulting in substantially more biomass accumulation by age 50. The pattern for a stand containing both conifers and alder showed annual production that matched that of the conifer stand, but much lower biomass accumulation. The difference in the accumulation of biomass between the stands with similar growth rates reflects the greater mortality of trees in the mixed stand. These shifts in dominance in multi-species stands, coupled with the importance of species in affecting rates of production and mortality, also underscores the challenge of deducing pollution impacts on forests.

Stand development

Stand development involves changes in forest structure (size, number of trees, species) over time. Trends depend on conditions at the time of stand origin, but typically follow general patterns that are mediated by disturbance, management, site quality, stand density and other factors. Most stands progress through recognizable stages as they age and develop, and a 4-stage model of stand development can be applied to most of the coniferous forests in the West (e.g., Oliver 1981, Peet and Christensen 1980, 1987, Long and Smith 1984, Peet 1988). Each stage is associated with characteristic patterns of tree establishment, growth, and death. A stand moves from the initiation stage immediately following a major disturbance, through thinning and transition stages, to reach the old-growth stage (Peet and Christensen 1987).

These normal stages of stand development are relevant to the evaluation of pollutant impacts from several perspectives. The impacts of pollutants likely differ among the stages because of changes in tree vigor and species composition across the stages, and because key life stages (such as seed production and seedling establishment) are more critical in some stages than others. The

assessment of pollution impacts is also greatly complicated by the dynamic nature of stands progressing through the stages of development; the identification of pollutant impacts must be made on top of a very dynamic set of normal changes occurring within forests.

Stand Initiation Stage

Following a major disturbance that removes most or all of the canopy of the previous forest, resource availability to establishing trees increases greatly. The rate of recolonization of the site by trees depends on the presence of surviving root systems, buried seeds, or input of seeds from surrounding forests. The relative importance of these sources of new trees depends on species, site conditions, and the nature of the disturbance. Competition between trees is slight (Long and Smith 1984), but competition with non-tree understory plants is often important. Productivity tends to increase rapidly as re-establishing vegetation quickly occupies the site.

The primary productivity of the ecosystem is divided among tree and non-tree vegetation. High rates of productivity found on disturbed fertile sites may occur largely in the non-tree component of the vegetation. Tree leaf area reaches a maximum at the end of the stand initiation stage, and is a key determinant of progress to the thinning stage (Long and Smith 1984).

The development of non-tree understory plants is probably greatest in the early period of the initiation stage, declining as the leaf area of trees increases. Understory species may increase again through the later transition and old-growth stages.

In the West, the initiation stage typically lasts for about ten years when the spatial extent of the disturbance is small enough to allow reseeding from surrounding forests. For larger disturbances, the stand initiation period often lasts more than fifty years (Peet 1988). On the most severe sites, especially near the elevational range of trees, stand initiation may be limited to episodes of favorable weather conditions for tree establishment. These favorable weather conditions may only occur sporadically, with intervals as long as 100 years (Means 1982).

Thinning stage

As stand leaf area reaches a maximum, continued domination of site resources by the most-vigorous trees leads to mortality of less-vigorous trees. The same pattern pertains to the decline of non-tree vegetation as the tree canopy and root system increase utilization of site resources. Where site conditions and the nature of disturbance leads to a prolonged stand initiation stage, the thinning stage may be bypassed. Examples include a natural stand or plantation with high mortality from disturbance or otherwise where the initial spacing is wide.

Stand development during the thinning stage is characterized by declining growth rates for many trees as competition among trees becomes more important, and by death of suppressed trees. In a

stand that passes relatively rapidly from the initiation stage to the thinning stage, the sudden decline in annual ring widths could be misinterpreted as the sudden onset of stress caused by pollution. In this case, the sudden stress results from competition among trees and the decrease in growth of individual trees does not represent a change in the rate of growth of the stand. In fact, growth rates of stands tend to reach a maximum during the thinning stage.

The death rate of trees typically continues at a constant per capita rate in unmanaged stands during this stage (Peet and Christensen 1980, 1987). The probability that a tree will survive (or die) during a given period is independent of the number of trees in the stand (the total number of tree deaths/ha would be greater in dense stands). In Douglas-fir forests, the annual rate of mortality ranges from about 5 to 8 trees per thousand, compared with 3 to 5 per thousand for ponderosa pine (Pinus ponderosa) stands (Franklin et al. 1987).

With the full utilization of site resources, establishment of new trees is uncommon during the thinning stage, unless cutting of trees substantially increases the resources available to establishing seedlings. As a stand progresses through the thinning stage, deaths of single trees create islands of resource availability that are too large to be readily occupied by surviving trees; this allows regeneration of species that tolerate low availability of resources (called shade-tolerant species, or simply tolerant species), and moves the stand into the transition stage. Unmanaged stands in the West commonly spend 50 to 100 yr in the thinning stage.

Transition stage

The transition stage is characterized by increasing unevenness in the stand, including uneven distributions of leaf area, age classes of trees, and distribution of site resources. Information on the dynamics of stand leaf area is sparse, but a decline relative to the thinning stage has been found in some cases (Aplet et al. 1989, Ryan 1990). The death of individual large trees takes on increasing importance during this stage. Stands dominated by single species may shift to multi-species, multi-storied structures. In some extreme cases, such as the old Douglas-fir forests of the Pacific Northwest, the death of a single dominant tree may represent an annual rate of mortality per hectare that matches or exceeds the rate of biomass increment on all other trees. As the accumulation of biomass in living trees declines, the old-growth stage is reached. The approach to old-growth conditions may take 200 years to over 500 years (Oliver 1981). In many parts of the West, the time between major disturbances is too short to allow most stands to move beyond the transition stage (Peet 1988).

Old-growth stage

The definition of old-growth is widely debated, but certain characteristics are commonly associated

with old-growth stands. The oldest age-class dominates the site, but as large trees die and fall, openings are created that allow the understory to flourish and grow into the canopy. The old-growth forest becomes a mosaic of large, old trees interspersed with the initiation, thinning and transition stages, which may persist in varying proportions until a large-scale disturbance occurs. The nature of old-growth mosaics is one of great variability, and classic ideas about steady state forest conditions at landscape scales may not be valid (Botkin 1989).

The accumulation of biomass in the old-growth stage is expected to be zero, or to oscillate between periods of increase and decrease, but few long-term studies are available to document this expectation. Grier and Logan (1977) estimated that the biomass increment of trees in a 450-year-old Douglas-fir forest in Oregon was about -4,000 kg/ha annually because of substantial mortality of large trees. Franklin and DeBell (1988) characterized the dynamics of an old-growth forest of Douglas-fir and western hemlock (Tsuga heterophylla) in Washington for a period of 36 years, and concluded that the distribution of size classes and species remained relatively constant, despite the death of 22% of the trees. The major causes of tree death were wind (accounting for 46% of the deaths) and suppression (40% of the deaths).

Stand Development and Ecosystem Processes in the West

Empirical data are not available to synthesize a picture of stand development through the four stages for most forest types in the West. Peet (1981, 1988) summarized patterns of stand development in the Front Range of Colorado for a favorable site (Figure 6.4a) and an unfavorable site (Figure 6.4b). On the favorable site, the initiation period is characterized by high rates of tree establishment, increasing biomass and production, and high species diversity. With the onset of the thinning stage, production plateaus as biomass continues to accumulate and species diversity and rates of tree establishment decline sharply. In the transition stage, productivity and biomass decline largely due to the mortality of large trees. Species diversity and tree establishment increase. The creation of larger gaps during the old growth stage allow a resurgence of productivity and biomass accumulation. On a less favorable site, the maximum rates of all four features of the stand are lower and the distinctions between stages become muted.

Changes in species composition are expected to be dramatic during stand development in many of the major forest types of the West, often including replacement of early dominant species such as aspen (Populus tremuloides) in parts of the Rocky Mountains or red alder in parts of the Northwest. In some cases, such as ponderosa pine forests in the southern Rockies, a single tree species dominates all stages of stand development. Environmental changes that would accompany these stand development sequences have not been well characterized, but some generalizations are

possible based on a variety of studies from around the West.

Several studies in the West support a primary role of leaf area and light interception in determining tree productivity and changes in understory light environments with stand development (Brix 1981, 1983, Waring 1983, Binkley and Reid 1984, Oren et al. 1987, Smith and Long 1989). For example, Gholz (1982) documented a strong relationship between aboveground net primary productivity and stand leaf area in a transect in Oregon of forests ranging from rain forests on the coast to pinyon/juniper stands east of the Cascade Mountains. He concluded that the effects of the diverse environments on forest productivity were mediated largely through effects on canopy leaf area. The leaf area of forests in the West ranges from near 0 m^2 of leaves (on a projected, or shadow-cast basis) per m^2 of ground area for newly regenerating forests, up to a maximum of about 10 to 13 m^2/m^2 for stands of shade-tolerant species such as Sitka spruce (Franklin 1988). The rate of leaf area development following major disturbances is highly variable, ranging from 6 to 50 years to reach maximum levels in many western forests (Zavitkovski and Newton 1971, Long and Smith 1984). Understory leaf area declines as the overstory canopy expands (Turner et al. 1978).

Changes through stand development also strongly influence temperatures within ecosystems. Canopies moderate fluctuations in temperatures at the soil surface, and reduce both daily highs and lows in comparison to disturbed sites. In a classic study of a Douglas-fir forest at the Lubrecht Experimental Forest in Montana, Hungerford (1980) measured the maximum and minimum temperatures on August 29, 1978 in stands that had received a variety of silvicultural treatments. The intact forest showed a daily maximum temperature of 35° C at the soil surface, and a daily minimum of 2° C, while the clearcut site had a high of 56° C (possibly lethal to seedlings), and a low of -5° C. The period between the last freezing temperature of spring and first freeze of autumn in the uncut forest was 112 days, compared with only 20 days in the clearcut site (Hungerford 1980).

Water use by forests also changes with stand development; studies of changes in forest hydrology following harvest document these changes. In Arizona, harvesting all ponderosa pine trees in a watershed increased streamflow by about 125 mm (equivalent to a layer of 125 mm of water across the entire surface of the watershed; Ffolliott and Thorud 1974). Factors contributing to the increase in runoff after harvesting include reduced interception loss from the canopy (evaporation before precipitation reaches the ground), and reduced transpiration by trees. Both factors lead to wetter soils, and presumably less moisture stress for remaining or newly established trees. At the Coram Experimental Forest in Montana, Newman and Schmidt (1980) followed the seasonal changes in soil moisture in plots with intact larch/Douglas-fir forests and in plots that had received various levels of

harvesting. The intact forest depleted soil moisture to below 15% (water weight/dry soil weight) during the summer, compared with a minimum value of 25% for the young forest regenerating in the clearcut. Increased soil moisture and water run-off may persist through decades of stand development (Troendle and Kaufmann 1987). Adams et al. (1991) compared soil moisture levels in a clearcut/burn and control area in the Oregon Cascade Range. The clearcut/burn area averaged higher moisture levels than the control area for the first few years. Within four years, however, the surplus moisture in the clearcut/burn area had declined to less than the control moisture level and remained less for over the next decade of monitoring. The deficits were attributed to a rapid increase in plant cover after the burn.

The rate of nutrient availability in forests depends primarily on the chemical quality of organic matter present in the forest floor and mineral soil, and on moisture and temperature conditions that affect the activity of decomposer microbes (Binkley 1986). All of these factors probably change with stand development, but few studies have characterized how changing microenvironmental conditions alter nutrient availability through stand development in the West. General expectations are that nutrient availability should increase after forest removal due to wetter and warmer soil conditions (Edmonds et al. 1989), and so far all studies in the West have shown higher nitrogen availability in younger forests (Binkley 1984, Matson and Boone 1984, Hart and Firestone 1989, Arthur 1990, Frazer et al. 1990, Page-Dumroese 1991).

Pollution Impacts at the Stand and Ecosystem Levels

The impacts of pollution on the growth of individual trees can be dramatic, ranging from moderate reductions in annual ring widths to complete absence of growth rings in the lower stem for some years (Chapter 7). Altered growth rates can lead to changes in patterns of tree death, species regeneration, and species composition. The effect of air pollution on the growth of stands is more complicated than the effects on single trees, because the reductions in growth of sensitive individuals may be partially offset by increased growth of less sensitive trees (Chapter 7).

Pollution Impacts on Species Composition

Pollutant impacts across stand development stages depends in part on the sensitivities of species to the pollutants. The effects of pollutants on individual tree performance depend on the balance between photosynthesis and respiration, and these effects differ among species (see Chapter 5). In the San Bernardino mountains (Chapter 12), the sensitivity to ozone pollution decreases in the order of: ponderosa pine, Jeffrey pine (Pinus jeffreyii), white fir (Abies concolor), Coulter pine (Pinus coulteri), incense cedar (Libocedrus decurrens), bigcone Douglas-fir (Pseudotsuga macrocarpa), and sugar pine (Pinus lambertiana). In response to accumulated ozone exposure, rates

of photosynthesis and stomatal conductance in ponderosa pine needles declined (Coyne and Bingham 1981), and annual radial growth declined from 5 mm yr^{-1} in healthy trees to 3 mm yr^{-1} in pollution impacted trees (McBride et al. 1975). The stands examined by McBride et al. (1975) differed substantially in structure (G. Reams, Oregon State University, personal communication), so differences in radial growth may not correspond to differences in growth at a stand level. The height reduction caused by ozone was about 2 m in otherwise comparable 30-year old trees. Height and diameter growth reductions combined to reduce merchantable wood volume from 0.55 m^3/tree to 0.14 m^3/tree (McBride et al. 1975). However, widths of annual rings from 1950 to 1975 increased in approximately one-third of the ponderosa pines measured in the San Bernardino Mountains at two locations that received high ozone exposures (Miller 1983). These growth increases may have resulted from decreased competition after the death of neighboring trees. Ponderosa pine trees were highly variable in sensitivity to ozone, and less resistant genotypes may have been eliminated from the forests over the past 30 years. This pollutant-induced thinning may have enhanced the vigor of the remaining, more resistant, individual ponderosa pine (Miller 1983) and trees of other species.

Important effects have been demonstrated of the role played by air pollutants in mediating or increasing pest and pathogen attacks in the West. Colonization of stumps and roots by the root rot fungus, Fomes annosus, was 30 to 50% faster in pine trees showing chronic ozone injury than pine trees not showing chronic ozone injury; controlled ozone fumigation of 6-year-old ponderosa and Jeffrey pine seedlings also increased fungal infection (James et al. 1980). In an area with high ozone levels, bark beetles (Dendroctonus brevicomis) were important agents in over 80% of the pine trees that died (Miller 1983). Bark beetles and defoliators can also be important pests because of other factors such as normal aging or changes in stand composition; pest presence does not necessarily indicate air pollution damage.

Air pollution during stand initiation can influence cone production, likelihood of seed regeneration, and susceptibility of seedlings to pollution impacts. Seed production in conifers varies with genotypes and level of stress. Stress may lead to short-term increases in seed production in some species whereas prolonged stress may reduce seed crops. Hedgecock (1912, cited in Smith 1990) found that conifers bore few or no cones near the Washoe smelter at Anaconda, Montana. Other studies have documented reduced cone crops near point sources of sulfur dioxide, and regions of high ozone pollution (Smith 1990). In the San Bernardino Mountains, dominant ponderosa pine and Jeffrey pine trees showing severe ozone damage produced significantly fewer cones than uninjured dominant trees (Luck 1980). However, acorn production by California black oak

(Quercus kelloggii) was not reduced by ozone exposure (Miller et al. 1980), suggesting the possibility of better regeneration of oak than pine.

Direct effects of acid deposition on seed germination are likely small (Smith 1990), as are effects of ozone (Hogsett et al. 1989). However, seedlings may be affected by both acids and ozone (Smith 1990, Hogsett et al. 1989).

Indirect effects of pollution may also be important in seedling establishment and growth, which are strongly influenced by the micro-environment at the soil surface. For example, reduced canopy leaf area in forests of southern California following ozone damage allowed more solar irradiance to reach the forest floor than in unaffected forest canopies, raising seed bed temperatures and seedling transpiration demands (Miller 1983). Despite these possible effects of ozone, McBride et al. (1985) found that the level of ozone exposure had no effect on the establishment of seedlings of ponderosa pine or white fir during a 10-year period in permanent plots along an ozone gradient in the San Bernardino Mountains. This case study illustrates that well-based expectations may not match real developments in forests.

During the thinning stage, pollution impacts may be particularly important. The dominating influence of tree-to-tree competition is probably most important in driving individual tree growth and mortality. Pollution-induced stress on trees of sensitive genotypes and species is likely to impair their ability to compete with less sensitive trees. No clear examples of pollution impacts at the thinning stage are available, but susceptibility of stressed trees to bark beetle attack was demonstrated experimentally for lodgepole pine in Oregon. Waring and Pitman (1983) used pheromones to attract large numbers of beetles to trees that had received treatments of fertilizer (to reduce stress) or carbohydrate (to tie up soil nutrients and increase stress). They found that the death of trees depended on the number of beetle attacks, and on the vigor of the tree. Tree vigor was indexed as the grams of wood produced per m^2 of tree foliage. High vigor trees survived relatively high numbers of attacks, whereas low-vigor trees were killed even by low numbers of attacks. A similar pattern may develop if stands in a thinning stage were exposed to pollution-induced stress.

Trees impacted by pollutants during the stand initiation stage would likely be at a competitive disadvantage during thinning stage. A drought or other stress would make them especially vulnerable. These trees would likely die during the thinning stage, but the growth of associated surviving trees may increase, keeping stand growth high.

During the transition stage, pollutant impacts might include acceleration of stand dynamics, increasing mortality of overstory trees and favoring establishment of new individuals. In the West,

pollution-induced changes in composition in the San Bernardino Mountains (see Chapter 12) fit this pattern, where impaired growth and greater mortality of ponderosa and Jeffrey pines may benefit regeneration of incense cedar. In this case, pollution stress increased susceptibility of the pines to bark beetles and root pathogens which were the direct causes of death. High mortality of pines may lead to dominance of the stand by species more tolerant of ozone, with potentially little effect on the total productivity of the stand.

Little empirical information is available on pollution effects on old-growth forests. Work in old-growth forests in the Seattle area has not detected pollution effects on growth rates (see Chapter 8 for work by Brubaker and others). Pollution effects might accelerate normal processes of tree death and replacement in a mosaic of stands in the old growth stage, but the effects could be more complicated. For example, pollution stresses could affect the survival and growth of both old, established trees and of newly regenerating seedlings. As surviving trees grow, changes in canopy and understory structure via tree death or minor disturbance provide surplus resources which allows seedling regeneration. The regeneration is typically shade-tolerant and grows slowly, depending on the resources available. Pollutant exposure may reduce seed sources, and weakened trees grow slower and become vulnerable to insects and disease. Environmental limitations become less intense as the canopy opens by tree deaths. All of this is speculative because good examples of pollution-impacted old growth forests do not exist in the West.

The effects of pollutants on stand structure, especially upon relationships between overstory and understory plants, may be complex. Early expectations were that large, dominant trees might receive greatest exposure and show greatest impacts; understory plants were expected to be less exposed and less affected (Woodwell 1970, Treshow and Anderson 1988). However, species sensitivity is often more important than pollutant dose, and generalizations about responses of overstory and understory plants may not be warranted. For example, Anderson (1966, cited in Treshow and Anderson 1988) examined the impacts of fluoride pollution around a phosphate plant in Idaho. Oregon
grape (Berberis repens), an understory herb, showed injury at lower exposure levels than the overstory Douglas-fir. Understory species that were more tolerant of ozone, such as grasses, were more plentiful in high-fluoride sites. Recovery of highly impacted sites since closure of the phosphate plant has been barely noticeable.

Pollution Impacts on Environmental Factors

The role of pollution in altering regimes of light and temperature in forest ecosystems depends strongly on changes in forest canopies. Reductions in canopy leaf area should reduce light

interception and allow greater soil temperatures, and greater fluctuations in diurnal and seasonal temperatures. The impact of pollution on environmental factors would likely differ across stand development stages. However, too little information is available to highlight these differences for us to separate our discussion by stand development stage.

As with temperature, the effect of pollutants on forest hydrology would be expected to relate strongly to changes in the forest canopy. Miller et al. (1980) noted that reductions in the leaf area of ponderosa pine trees resulted in greater penetration of rainfall to the soil surface, lowering interception losses from the canopy but probably increasing evaporation from the surface of the forest floor. They also pointed out that ozone-impacted needles showed reduced stomatal conductance per unit of leaf area, reducing transpiration by impacted trees. Whether transpiration of the entire stand would be reduced depends of course on the ability of neighboring trees to increase their rates of transpiration. If overall stand transpiration were lower, increased soil water availability may allow less affected plants to transpire more, increasing their exposure (via open stomata) to ozone (Miller 1983).

The direct effects of air pollution on nutrient availability have received little attention in the West, and for the most part only speculations are possible. A wide range of effects can be postulated. For example, deposition of nitric acid to nitrogen limited soils might increase nitrogen availability (see Chapter 4). Nitrogen deposition is poorly characterized in the West (see Chapter 3), though we do know that deposition of nitrate and ammonium in rain and snow is generally low. No dramatic, or perhaps even measurable, effect on nutrient cycling is currently expected from acid deposition, except perhaps in southern California where deposition rates are high (Chapter 3).

Some indirect effects of oxidant pollution on nutrient cycling may also occur, including greater needlefall rates (at least temporarily) and altered concentrations of nutrients (see Chapters 4 and 12). The importance of such changes to the rate of nutrient availability and other processes remains unknown. Long-term changes in ecosystem structure following air pollution exposure can also influence nutrient cycling. Changes in species composition could lead to species-driven changes in nutrient cycling patterns; but again no evidence is available to support speculations. Perhaps more critical would be increased fire risk that might result from greater accumulation of fine fuels in pollution stressed stands. Greater fuel loads coupled with greater drying due to increased light penetration could alter both the frequency and intensity of fires. Changes in fire characteristics would have large impacts on nutrient losses, cycling and availability (Binkley and Christensen 1991).

Synthesis

Pollution response classes

A classification scheme was developed by Smith (1974, with modifications in Smith 1981, 1990, and Bormann 1985, 1990) to describe classes of forest response to increasing pollution stress. In Class I, pollutant levels are generally low, and ecosystems serve as both sources (hydrocarbons) and sinks for low levels of pollutants. Forests remain relatively unaffected, or may even benefit from slight fertilization effects. Most of the West currently falls in this class.

Early in Class II pollutant levels begin to interfere with some aspects of the life cycle of sensitive species or individuals. Plants are either adversely affected or their growth is enhanced because of adverse effects on other plants. Pollutants inhibit photosynthesis, and reduces available carbohydrate reserves needed for reproduction or defensive mechanisms. Portions of the West could fall within the early Class II category, but normal dynamics of forests are large enough relative to such pollution-induced changes that detection is almost impossible. Portions of the southern Sierra Nevada probably fall within early Class II (Chapter 11), and perhaps portions of southern Arizona (Chapter 10). With increasing pollution, Class II responses would include declines in populations of sensitive species. Some individuals of sensitive species may survive, and decreases in pollution levels would allow sensitive species to recover. Shifts in species dominance may maintain total ecosystem function (such as net primary production) at levels similar to unpolluted conditions, although structural changes (such as species composition or canopy distribution) would occur. Some of the forests of the San Bernardino Mountains in southern California show more pollution damage than any forests in North America (with the possible exception of the forests around Mexico City), and fall into the severe end of Class II (see Chapter 12).

Bormann (1985, 1990) stressed that forests in Class II begin to lose redundancy, or the capacity to respond flexibly to new stresses. For example, pollution stress may reduce the genetic variability within populations by removing sensitive individuals, and this reduction in genetic diversity may impair the population's ability to cope with other stresses such as drought or insect outbreaks. Similarly, the removal of sensitive species from a diverse forest may constrain the ability of the forest to respond to changes in climate. Losses in redundancy may be difficult (or impossible) to detect, but may be fundamentally important to the ecosystem response to both natural and pollution-related stresses.

In Class III, greater pollution stress results in major disruptions of the forest. Productivity declines, biotic regulation of nutrient cycles weakens, and some species disappear. Later recovery of the forest (if pollution levels declined) could be impaired by a lack of propagules for many species. Examples in the West are limited to point sources of pollution, such as the aluminum ore reducing plants at Columbia Falls, Montana and Franklin Park, Washington (Smith 1990).

The symptoms characterizing the stages of forest ecosystem decline depend in part on the stage of stand development. A matrix can be constructed to show the interactions between stage of stand development and stage of ecosystem stress (Table 6.1). The movement of a forest ecosystem through time may be vertically through Table 6.1 if pollution levels are constant; horizontal to the right or diagonally to the lower right if pollution levels are increasing; or potentially to the left or lower left if pollution levels were declining. Trends for ecosystems within Class I are summarized from the discussion earlier, and those in Class II represent slight modifications that include primarily shifts in species dominance and perhaps composition. Pollution effects may be severe enough in Class III to shorten or preclude some of the stand development stages.

Two major challenges confront research and management of forests in polluted environments:

--Detecting shifts of ecosystems from Class I to Class II; and

--Predicting (and modifying?) the further changes in ecosystems that fall within Class II.

Substantial pollution-induced changes may occur in a forest in Class II that are difficult to separate from the normal changes that we've described with stand development, including patterns for single trees, for species within stands, and for entire forests. Bormann (1985, 1990) raises a series of sobering questions about the impacts of a 10% reduction in productivity resulting from pollution stress, including issues of species diversity, soil erosion, and nutrient retention. In most cases, a 10% reduction in net productivity may go undetected, and we cannot predict whether consequences for ecosystem structure and function would be small or large. The dendrochronological studies described in the following chapters attempt to detect unusual changes in tree growth which might be pollution related. The second issue of predicting further changes where pollution impacts are detected remains largely a mystery in the West and around the world.

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Table 6.1. Interaction of stages of stand development and ecosystem stress.

Stand Development Stage	Forest Stress Class I	Forest Stress Class II	Forest Stress Class III
Stand Initiation	Regeneration by seed, sprouting; competition between trees and non-tree vegetation; rapid expansion of canopies and root systems	Subtle shifts in species success in regeneration; shifts in competitive success alter growth rates, with some species improving at expense of others	Substantial changes in species success, with dominance of pollution resistant species; reduced growth of most species; slower expansion of canopies and roots
Thinning	Maximum leaf area attained, mortality increasing from competition between trees, maximum productivity	Maximum leaf area attained, but proportion from resistant species greater, competition induced mortality with greater rates in sensitive species but similar overall rate	Leaf area reduced, mortality driven by competition, pollution stress and pathogens; in severe case, thinning stage may be bypassed
Transition	Increased variation in canopies allowing reinitiation of seedling establishment; high productivity	Very similar, with possible differences in species composition and dominance	May occur sooner as pollution stresses disaggregate canopy; low productivity
Old-growth	Mosaic of age classes, diverse stand structure, low or negative net productivity	Very similar, with possible differences in species composition and dominance	Uneven structure with partial or complete removal of dominant trees; stage may not occur if severe enough, with site moving to stand initiation stage

Figures

Figure 6.1. Accumulation (upper) and growth rate of height, radius, and volume (lower) for a single Douglas-fir tree on a dry site in Oregon (from data supplied by J. Means, U.S.D.A. Forest Service).

Figure 6.2. Relative rate of volume growth for the Douglas-fir tree from Figure 6.1 compared with expected rate for an entire stand with a site index of 40 m at 100 yr (from yield tables of McArdle et al. 1961).

Figure 6.3. Annual rate of biomass accumulation (top), mortality (middle), and total biomass accumulation (bottom) for adjacent forests of red alder, conifers, and mixed alder and conifers. RA=red alder, DF=Douglas-fir, SS=sitka spruce, WH=western hemlock (from Binkley and Greene 1983).

Figure 6.4 Generalized development patterns for Colorado Front Range forests; A is typical of lodgepole pine and Douglas-fir forests, and B is more representative of high-elevation spruce-fir forests (from Peet 1988).

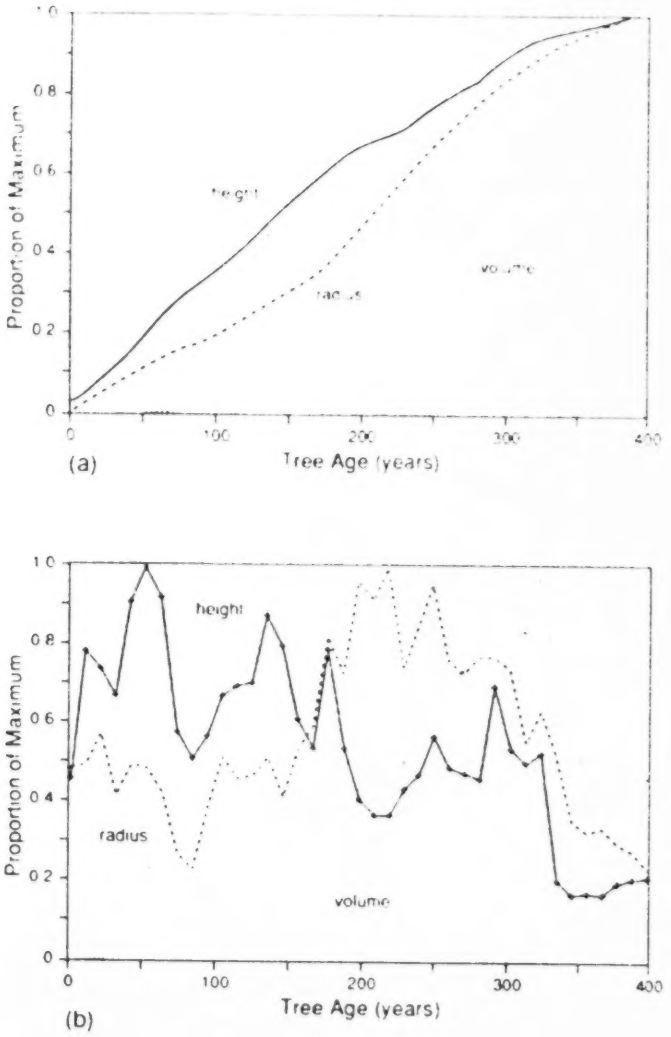

Figure 6.1 Accumulation (a) and growth rate (b) of height, radius, and volume for a single Douglas-fir tree on a dry site in Oregon (from data supplied by J. Means, U.S.D.A. Forest Service)

Figure 6.2 Relative rate of volume growth for the Douglas-fir tree from Figure 6.1 compared with expected rate for an entire stand with a site index of 40 m at 100 yr (from yield tables of McArdle et al. 1961).

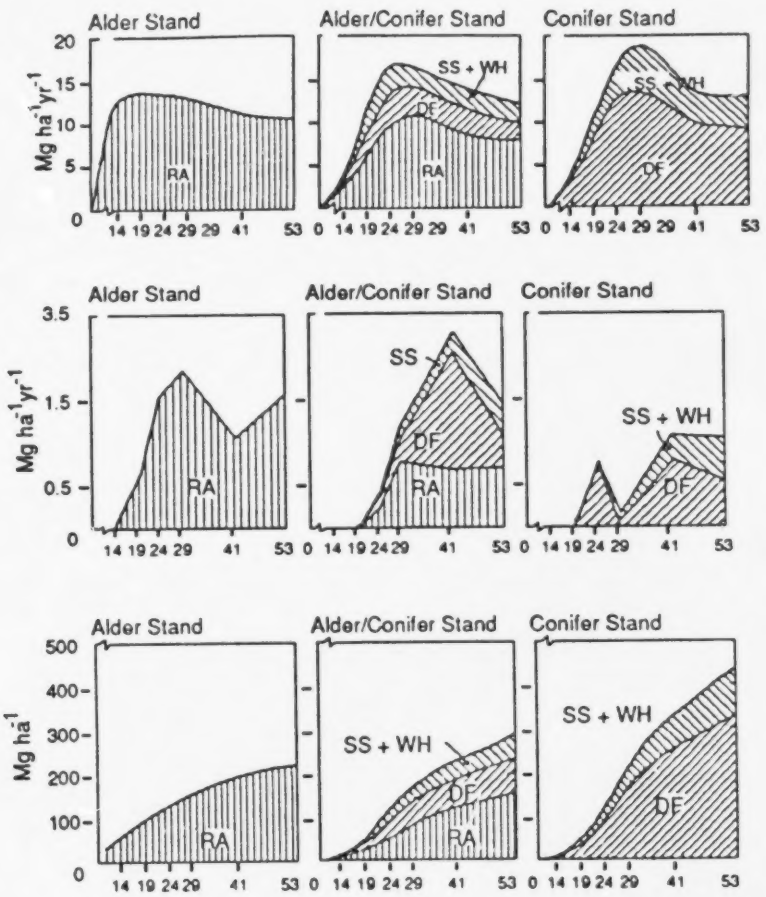

Figure 6.3. Annual rate of biomass accumulation (top), mortality (middle), and total biomass accumulation (bottom) for adjacent forests of red alder, conifers, and mixed alder and conifers. RA=red alder, DF=Douglas-fir, SS=sitka spruce, WH=western hemlock (from Binkley and Greene 1983).

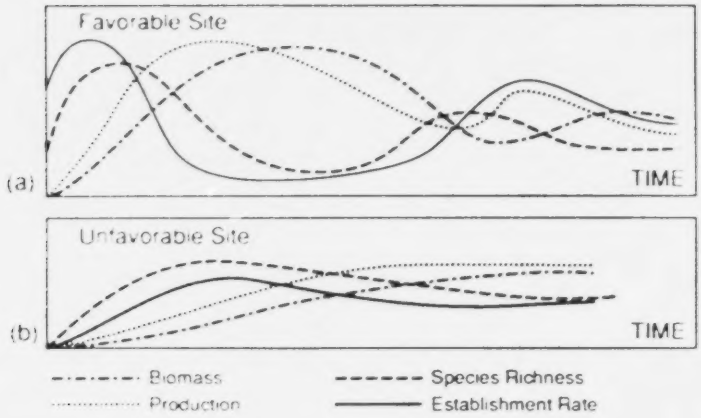

Figure 4. Generalized development patterns for Colorado Front Range forests. (a) is typical of lodgepole pine and Douglas-fir forests, and (b) is more representative of high elevation spruce-fir forests (from Peet 1988).